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THE EFFECT OF VARIOUS FOOD PLANTS ON SURVIVAL AND GROWTH RATE OF PIERIS[1]

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THE CLOSE RELATIONSHIP between most phytophagous insects and their host plants is a general phenomenon known by most entomologists. This relationship is so outstanding that field naturalists can often locate colonies of any particular insect most readily by first searching out the host plants, as they often are larger and more obvious to the eye than the insects themselves.

What is not so well known is (1) the extent to which it is possible for any particular species or race to survive on various food plants, and (2) the causes of the attraction to, and survival of, any race of insect on a particular plant.

It is the purpose of this paper to indicate something of the range of ability to survive of two insects, *Pieris rapae and Pieris protodice,* (the "cabbage or mustard "butterflies) on various cruciferous plants. In other papers, it is intended to go into the various aspects of the development of food plant preferences in insects, including its causes, evolution, and relationship to origin of phylogenetic groupings.

THE MATERIAL AND METHOD

The experimental work to be reported on here and in subsequent papers has been carried out in Arcadia, Southern California. All species of the genus *Pieris* (Lepidoptera: Pieridae) found in southern California have been utilized for the study. The geographical ranges and specific food plants of the species existing in southern California are being described elsewhere (Hovanitz, 1962) and the general distribution of the species of North America in another paper (Hovanitz, 1962). Five species of *Pieris* exist in this area, *P. rapae* (a European immigrant), *P. protodice, P. beckeri, P. sisymbrii* and *P. napi.* Each of these occupies a specific habitat and is restricted to a different food plant.[3]

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[3]Some taxonomists consider *Pieris occidentalis* to be a distinct species separate from *Pieris protodice,* rather than a geographical race, ecological race or local phenotypic form. If this were the case, there would be six species in southern California.

Pieris rapae is the easiest species to breed under greenhouse conditions and has been used for most experiments. It aslo has a wider range of satisfactory food plants than the others. As a European immigrant, it remains restricted largely to plants of European origin and has never adapted itself under natural conditions to any American native. Contrariwise, *Pieris protodice,* a native species, has never adapted itself to any European plant grown in cultivation, but has assumed an "economic" role only in utilization of European plants (mustards) growing in semi-wild habitats. The other *Pieris* are restricted entirely to one or a few native species of plants.

The food plant tests were made in several series at different times of the year and with different species of plants. Each series was run for the purpose of comparing the influence of several plants (usually five) on growth rate and mortality. For each series, a group of twenty larvae, obtained as follows, were grown on each plant. Female *Pieris rapae* were allowed to oviposit on a kale plant in the greenhouse. For the first series, the eggs were removed from the kale leaf and placed on leaves of the plant being tested in a petri dish. On all other tests, the eggs were allowed to hatch on kale, and to eat on it for one or two days before removal to the tested plants. In order to minimize the effects of variable environmental conditions, all tests of a series were grown at the same time and place. For example, eggs laid on September 11, 1959, were used for the first test. On September 14, 1959, the larvae were measured for the first time, and then successively thereafter each day until pupation. The dates of larval (or pupal) deaths were noted.

The later tests were similar except that (1) the origin of the parents was different, (2) one or two day old larvae were used instead of eggs, (3) the time of year and (4) place of breeding was different. Data on origin of the material for each test are indicated in Table 1.

TABLE 1: Source of larvae used in these experiments.

Series	Species	Food Source	Locality collected	Date of experient	Generations from wild
1	*Pieris rapae*	Cabbage	Western Orange County	Sept. 11, 1959	1
2	"	"	"	Oct. 9, 1959	2
3	"	"	"	Nov. 25, 1959	4
4	"	"	"	Feb. 20, 1960	6
5	"	"	"	Feb. 20, 1960	6
6	"	"	"	Aug. 2, 1960	11
7	"	"	"	Sept. 19, 1960	12
8	*Pieris protodice*	Mustard	Laguna Beach	Aug. 27, 1959	1
9	"	"	San Fernando Valley	July 18, 1960	1
10	"	*Cleome*	Owens Valley	July 21, 1960	1

SERIES NO. 1

Series No. 1 was conducted for the purpose of comparing the effect of the following plants on growth rate, size and mortality: black mustard (*Brassica nigra*), garden nasturtium (*Tropaeoum majus*), bladder pod (*Isomeris arborea*) and watercress (*Nasturtium officinale*) (Table 2). The females used for the source of larvae were obtained from an open cabbage field isolated from any other cruciferous food plant source and over which the adults were swarming in huge numbers. The probability that they came from any other source is infinitesimal.

TABLE 2. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 1).

Plant	Number	Number and percent of larvae died		Days from egg to pupation	Range of variation in larval growth
Nasturtium	20	16	50%	20	3
Kale	20	2	10%	12	2
Mustard	20	8	40%	13	3
Watercress	20	18	90%	17	1
Nasturtium	20	16	80%	18	5
Isomeris	20	10	50%	20	3

The mortality (Table 2, Series 1) was highest on watercress (90%), next highest on garden nasturtium (80%), then Isomeris (50%), mustard (40%) and least on kale (10%). The rate of development as determined by the first larva to pupate, was most rapid on kale (12 days), least rapid on Isomeris (20 days), and increasingly more rapid on nasturtium (18 days), watercress (17 days) and mustard (13 days). The range in variation of larval growth was greatest for nasturtium, since five days elapsed between the first larva to pupate and the last. The range as indicated in the table should be interpreted with the fact in mind that only a fraction of the original twenty larvae remained at the time of pupation. In other words, only two larvae pupated out of twenty that were fed on watercress. Had more survived, the range between the dates of pupation might have been greater.[4]

The growth rates of the larvae on the various plants were obtained by measuring ten larvae of each group each day and obtaining the average length. These were then plotted and a curve drawn for each. These curves are shown in Figure 1.

Measurements of the larvae were started on the third day after hatching as they were so small prior to that time. However, great

[4]It should be noted that the watercress used in these experiments was obtained by purchase in a food market while all other plants were grown in the laboratory. It has occassionally been found that despite repeated washings, insecticide residues may be present upon such commercial vegetables and that these may cause death of larvae feeding upon them.

differences already were apparent between the larvae grown on the various plants. Those on kale were 4.7mm long as compared with those on Isomeris which were only 1.5mm long. Those on nasturtium were 1.8mm, those on watercress were 1.9mm and those on mustard were 3.9mm. The kale-group larvae were over three times the size of the Isomeris group larvae. Increase in size of the larvae on subsequent days was fastest when the larvae were grown on kale, second fastest on mustard, and about equally as poor on each of the other three plants. The largest sized larva was that grown on Isomeris (24mm) as compared with that on kale (22.2mm) but after eight more days of larval life. Those on watercress and nasturtium pupated at 20mm and those on mustard at 17.9mm.

It appears that the greatest proportional size difference in the larval groups occurred during the first three days, but that most of the loss in size was later recovered by a longer growth period.

SERIES NO. 2

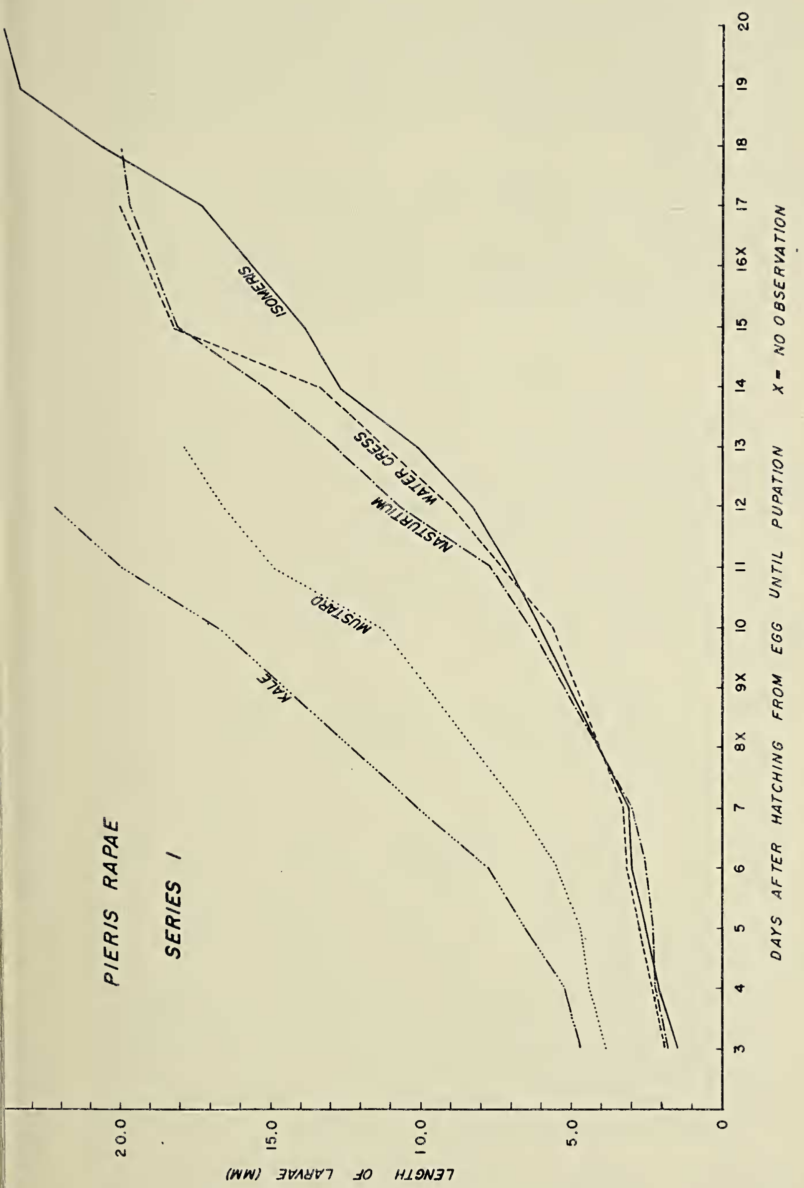
The tests of Series No. 2 were carried out in order to correct what were thought to be defects in the experiments of Series No. 1. These were two in number. The first was the high mortality in the eggs when they were removed from kale and placed on the other plants. This problem was averted by letting the larvae hatch on the kale plant before moving to the tested plants. The second presumed defect was the possibility of increased mortality of the very young larvae on the new plants, due solely to physical characteristics, toughness, etc. This was partially averted by allowing the larvae two days of feeding on kale before transference to the tested plants.

One change in food plant was made in this test: radish obtained from a food market was employed in place of watercress. Another inevitable change was the climatic condition under which the tests were conducted. They were changed slightly by the fact that the tests were carried out starting October 9, 1959, instead of September 11, 1959.

TABLE 3. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 2).

Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Kale	20	2	10%	0	0	2	10%	11	2
Mustard	20	2	10%	3	15%	5	25%	13	4
Radish	20	8	40%	5	25%	13	65%	13	5
Nasturtium	20	8	40%	2	10%	10	50%	14	5
Isomeris	20	12	60%	3	15%	15	75%	15	3

The mortality (Table 3) in this series was generallly not so high



1. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 1).

as in the series just preceding, though that on kale was the same at 10%, those on mustard dropped from 40% to 10%, on nasturtium dropped from 80% to 40% and on Isomeris increased from 50% to 60%. Watercress was not tested this time but instead radish[5] was used, with a resulting mortality of 40%. The better survival of these larvae is probably correlated with the fact that they were all grown during the first two days on kale.

Generally, the time (minimum days) to pupation in this series has been decreased (Fig. 2). The time on kale has been decreased one day, on mustard it remains unchanged, and on nastrutium and Isomeris it has been reduced five days. These reductions are probably correlated with the more successful survival of the young larvae on kale for the first two days, as compared with Series No. 1.

SERIES NO. 3

The tests of Series No. 3 are identical with those of Series No. 2 with the exception that they were started November 25, 1959 instead of October 9, 1959; in addition, the larvae by this time were four generations removed from the wild and inbred.

The larval mortality for all plants other than nasturtium was increased considerably in Series No. 3 compared with Series No. 2; 10% to 30% for kale, 10% to 35% for mustard, 40% to 80% for radish and 60% to 75% for Isomeris (Table 4). The data are comparable for the percentage of pupae died.

TABLE 4. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 3).

Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Kale	20	6	30%	0	0	6	30%	15	2
Mustard	20	7	35%	0	0	7	35%	16	5
Radish	20	16	80%	1	5%	17	85%	19	4
Nasturtium	20	7	35%	1	5%	8	40%	16	6
Isomeris	20	15	75%	2	10%	17	85%	18	8

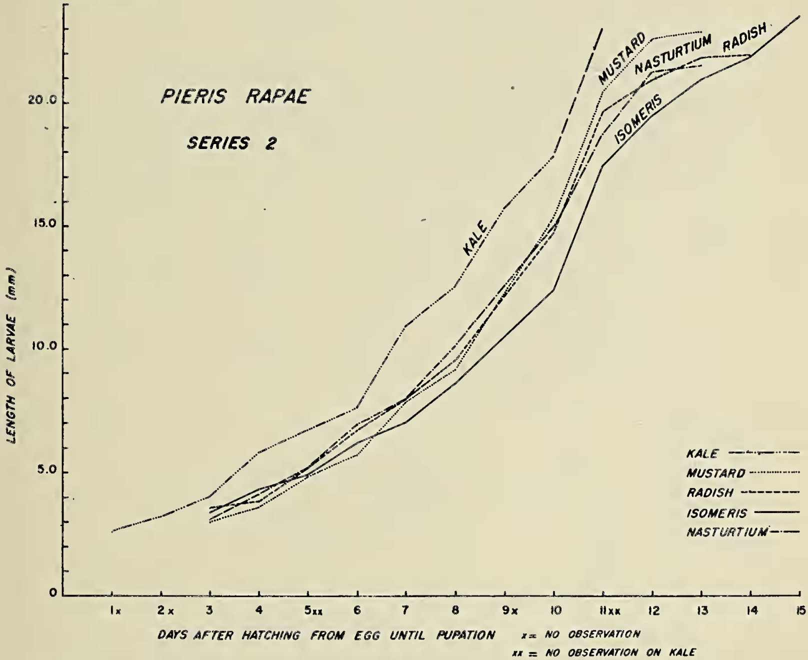
The length of larval life has also been increased considerably in Series No. 3 tests, and thus also the range of variation in larval growth.

The reasons for these differences between Series No. 2 and No. 3 are probably two fold. First, the later time in the season has meant that the conditions of growth were somewhat different, primarily in the temperature.

The larvae were grown in a greenhouse in which the temperature was not well-regulated. Therefore, the temperature of the October

[5]The radish used in this particular experiment, but not in others reported on by us, was obtained in a food market. Refer to footnote (4) for possible latent effects.

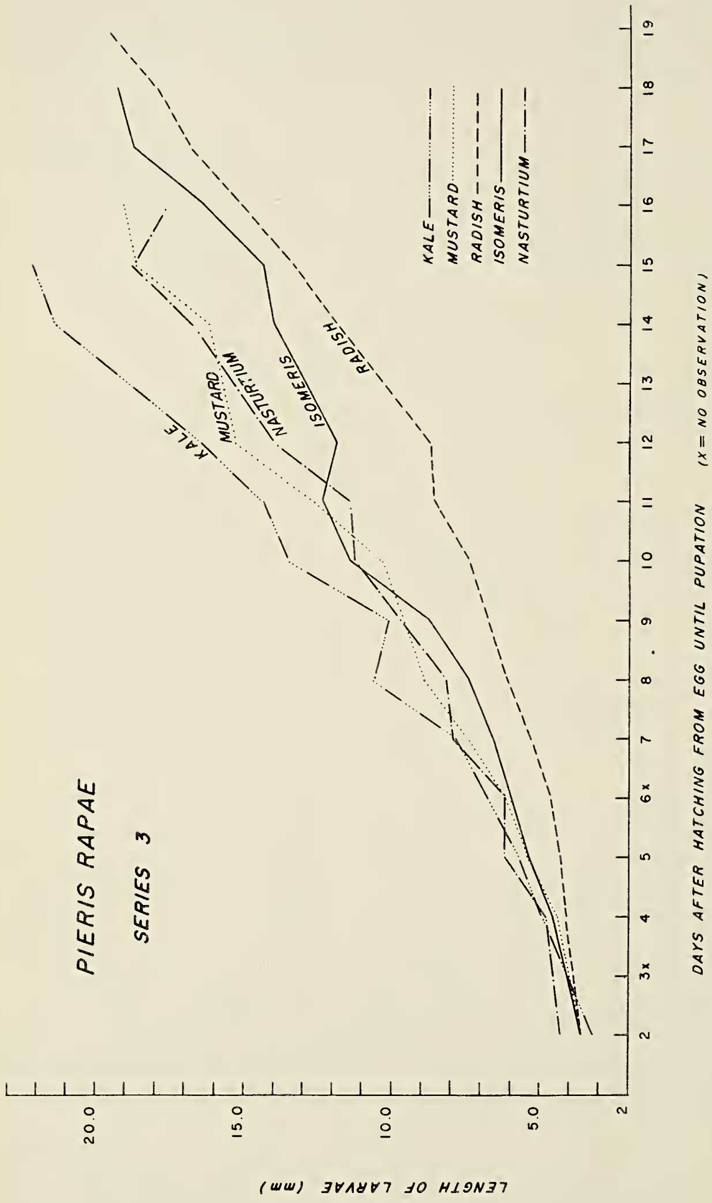
tests (Series No. 2) was higher than for the November tests (Series No. 3). This would profoundly influence the results insofar as the absolute growth rates are concerned. On the other hand, it did not affect the relative growth rates on the various food plants. These are still in the same descending order: kale, mustard, radish, nasturtium and Isomeris.



2. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 2).

The differential increase in size of the larvae on the various food plants is better shown in Series No. 3 (Fig. 3) than in Series No. 2 (Fig. 2). This is because the slower development rate served to exaggerate the differences between each strain. The larvae grown on kale grew larger at a faster rate than the larvae on any other plant, followed by mustard, nasturtium, Isomeris and radish. In Series No. 2, the order of the latter two were reversed. It is interesting to note that the ultimate size of the larvae which grew slowest was seldom equal to the size of those larvae which grew fastest. In fact, there is almost a direct relationship between these events.

A second reason for the difference between the mortality and growth data of these two series may be of genetic significance. The extent of inbreeding in the laboratory population by the fourth generation would have been sufficient to (a) increase the mortality, (b) slow



3. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 3).

development rate, (c) decrease size, (d) magnify the difficulties of feeding on abnormal plants by the simple means of decreasing overall vigor by the accumulation of allelic recessive lethal genes in the laboratory strain which had not yet had a chance to be eliminated by the selective effects of homozygosity.

SERIES NO. 4 AND 5

Series No. 4 was a test to compare various garden vegetables for their usefulness to *Pieris rapae.* These vegetables were mustard, kale, kohlrabi, broccoli and brussels sprouts. Series No. 5 was a similar test for various other plants. These were mustard (as before), nasturtium, radish, turnip and Isomeris. The tests were made in two series on February 20, 1962, using larvae following six generations of inbreeding, but of the same strain as used heretofore. In both of these tests, the larval mortality was higher on comparable plants used in previous tests. This again was probably due to the effects of inbreeding.

TABLE 5. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 4).

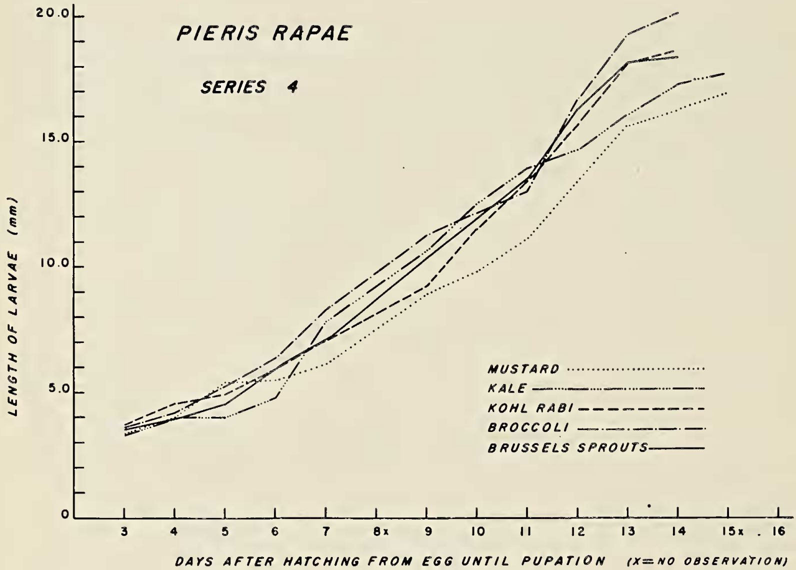
Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	9	45%	0	0	9	45%	15	9
Kale	20	5	25%	2	10%	7	35%	15	10
Kohl Rabi	20	9	45%	0	0	9	45%	14	9
Broccoli	20	9	45%	0	0	9	45%	14	9
Brussels Sprouts	20	10	50%	0	0	10	50%	14	9

In Series No. 4 (Table 5), the data show that the larvae on kale had the lowest mortality rate (25%) while all the other plant tests were about the same (45-50%). Despite this, however, larvae from kohlrabi, broccoli and brussels sprouts reached pupation ahead of those on kale or mustard.

TABLE 6. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 5).

Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	9	45%	0	0	9	45%	15	9
Nasturtium	20	19	95%	0	0	19	95%	16	—
Radish	20	14	70%	2	10%	16	80%	15	13
Turnip	20	13	65%	0	0	13	65%	15	4
Isomeris	20	12	60%	0	0	12	60%	18	14

In Series No. 5 (Table 6), the data show that the lowest mortality again was on mustard but with considerably higher mortality on the other plants: for example, 95% on nasturtium, 70% on radish and 60-65% on turnip and Isomeris. The length of larval life was longest on Isomeris (18 days) and about the same (15-16 days) on other plants. The range of larval growth period varied greater with radish and Isomeris than with any of the other.

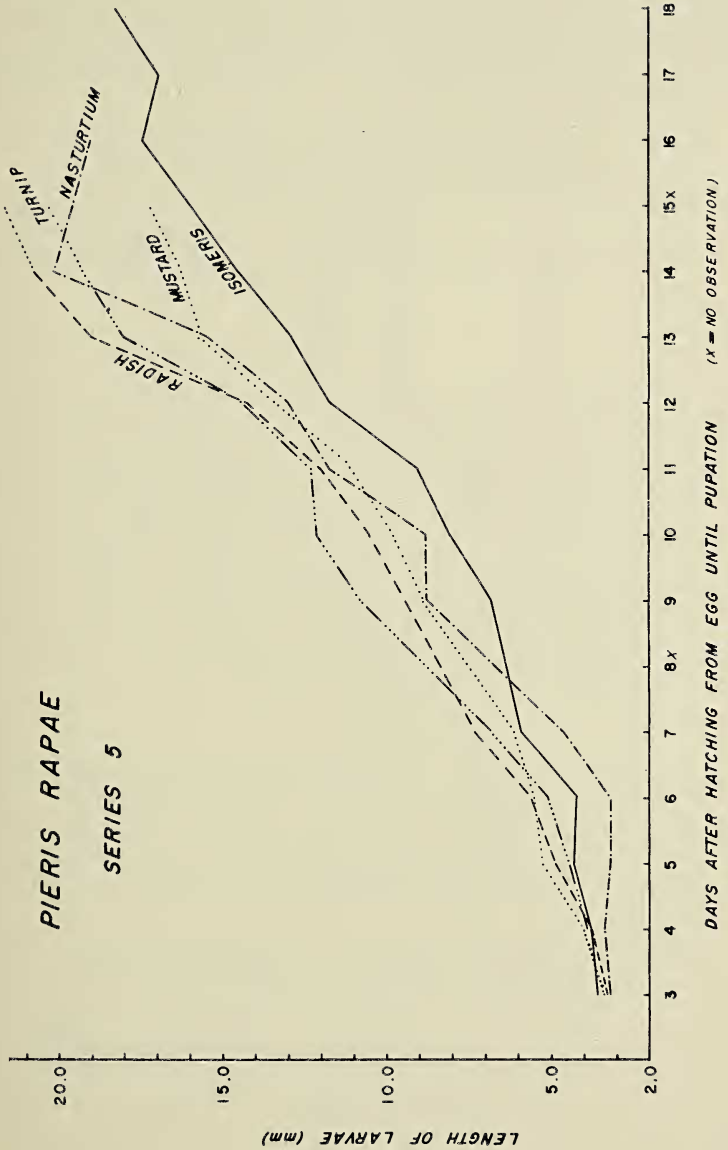


4. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 4).

The rate of increase in size (Fig. 4) was more rapid with broccoli, kohlrabi and brussels sprouts than with kale and mustard. It is believed that this may be correlated with a more turgid or water-content condition of these plants as compared with the drier or stiffer condition of the kale and mustard. For some reason, in Series No. 5, also, the increase in size of the larvae was not up to expectations on the mustard since the larvae on radish, turnip and nasturtium all exceeded those on mustard in final size (Fig. 5).

SERIES NO. 6

Series No. 6 was tested on August 2, 1960 with the use of larvae eleven generations from the wild. One new plant, (*Cleome lutea*), was tested in this series, since this plant was found to be primary food plant for *Pieris protodice* in Owens Valley, California. Mortality data



5. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 5).

for kale , mustard, nasturtium and Isomeris, (Table 7) compared well with previous data obtained on these plants (Series 1, 2, 3, 4 and 5). *Cleome* was only slightly less effective in maintenance of larval life, the mortality rate being 30% as compared with 20% for kale and mustard. The relative lengths of larval life and the range of variation in larval growth also compares favorably with previous data. The higher mortality as seen in Series 3, 4, 5 and 6 has here been reduced to nearly the level of Series No. 1.

TABLE 7. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 6).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Kale	20	4	20%	12	3
Mustard	20	4	20%	13	3
Nasturtium	20	10	50%	13	3
Cleome	20	6	30%	14	5
Isomeris	20	12	60%	18	6

The differences between growth curves for each of the plants tested has been greatly increased in this test as compared with earlier tests. The factors responsible for this are unknown but may be due to a reduced adaptability caused by increased homozygosis (Fig. 6).

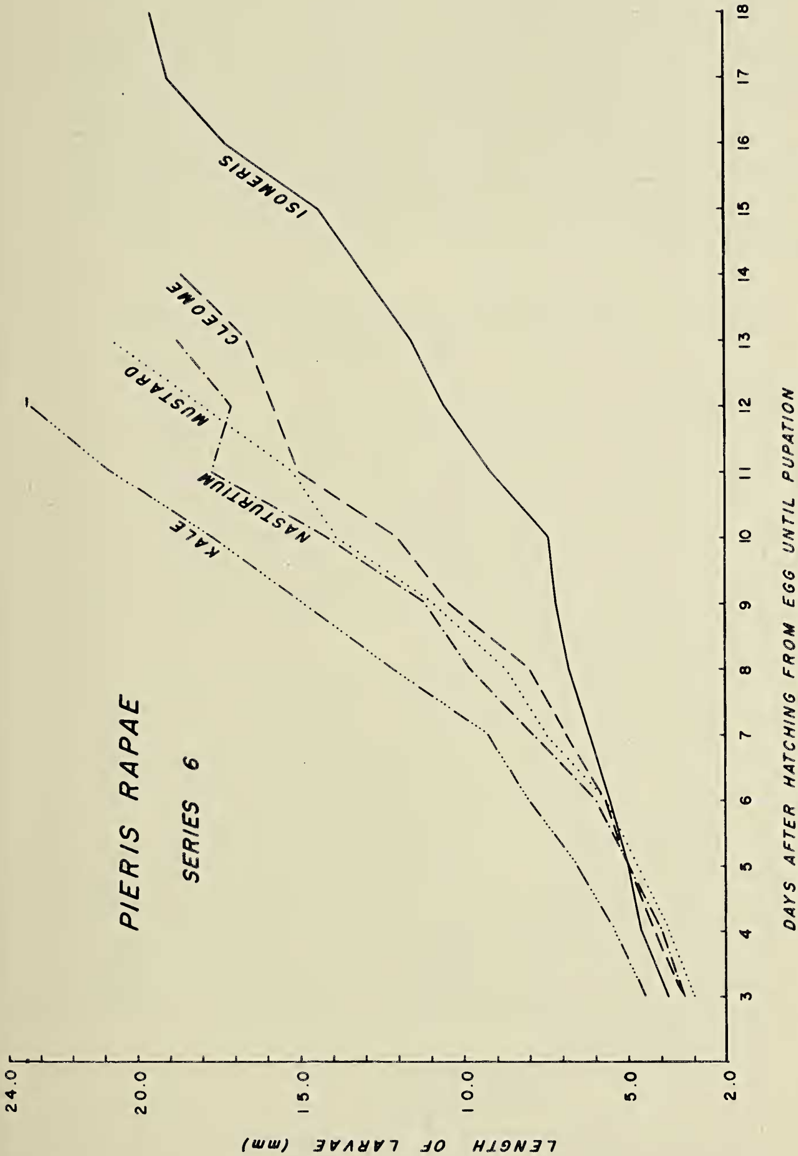
The larvae on kale were larger than those of any other plant at all times during their growth period. Pupation occurred the twelfth day. The larvae grown on nasturtium were almost the same size as those grown on mustard, whereas in Series No. 1 (Fig. 1) the larvae on mustard grew faster and larger. The larvae on *Cleome* were fourth in size on any day, while those on Isomeris were fifth.

SERIES NO. 7

This series was conducted in order to place the plant *Thelypodium affine* into position relative to the other standard test plants in the laboratory. *Thelypodium affine* is a native cruciferous plant from the desert regions which is not known to be a food plant of any *Pieris* species, though another *Thelypodium* species is the food plant of *Pieris sisymbrii.*

TABLE 8. Viability and growth rate of *Pieris rapae* grown on different kinds of food plants (Series 7).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Kale	20	5	25%	16	3
Mustard	20	6	30%	17	4
T. affine	20	14	70%	22	5
Isomeris	20	12	60%	18	6
Nasturtium	20	8	40%	17	6



6. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 6).

The tests of Series No. 7 (Table 8) were carried out on September 19, 1960, using larvae after twelve generations of laboratory inbreeding and growing on kale. The larvae grew relatively well on mustard, kale and nasturtium. The effectiveness of Isomeris was as previously tested. *Thelypodium affine* was the poorest of all these plants as far as effectively providing the larva with stimulation to feed.

The mortality of the larvae on *T. affine* was 70% as compared with 60% on Isomeris, 40% on nasturtium, 30% on mustard and 25% on kale. The length of larva life was increased from 16 days on kale to 22 days on *Thelypodium.* The final size of the larvae was reduced from 22mm long on kale to only 18mm long on the *Thelypodium* larvae which survived. (Fig. 7).

GENERAL OBSERVATIONS ON PIERIS RAPAE TESTS

The seven series of tests on *Pieris rapae* larvae have indicated several significant points:

(1) Larvae from strains grown previously on cabbage or kale have a lower mortality rate, have a faster development rate, and a greater size when grown on kale than when grown on any other plant tested. When similar larvae are grown on mustard, these factors are decreased slightly. The order of decrease for plants other than these two is in the order approximately as follows: nasturtium, *Cleome,* radish, Isomeris, and *T. affine.* Plants of the cabbage group: kohlrabi, broccoli and brussels sprouts, are about the same as cabbage or kale. Turnip is about the same as radish.

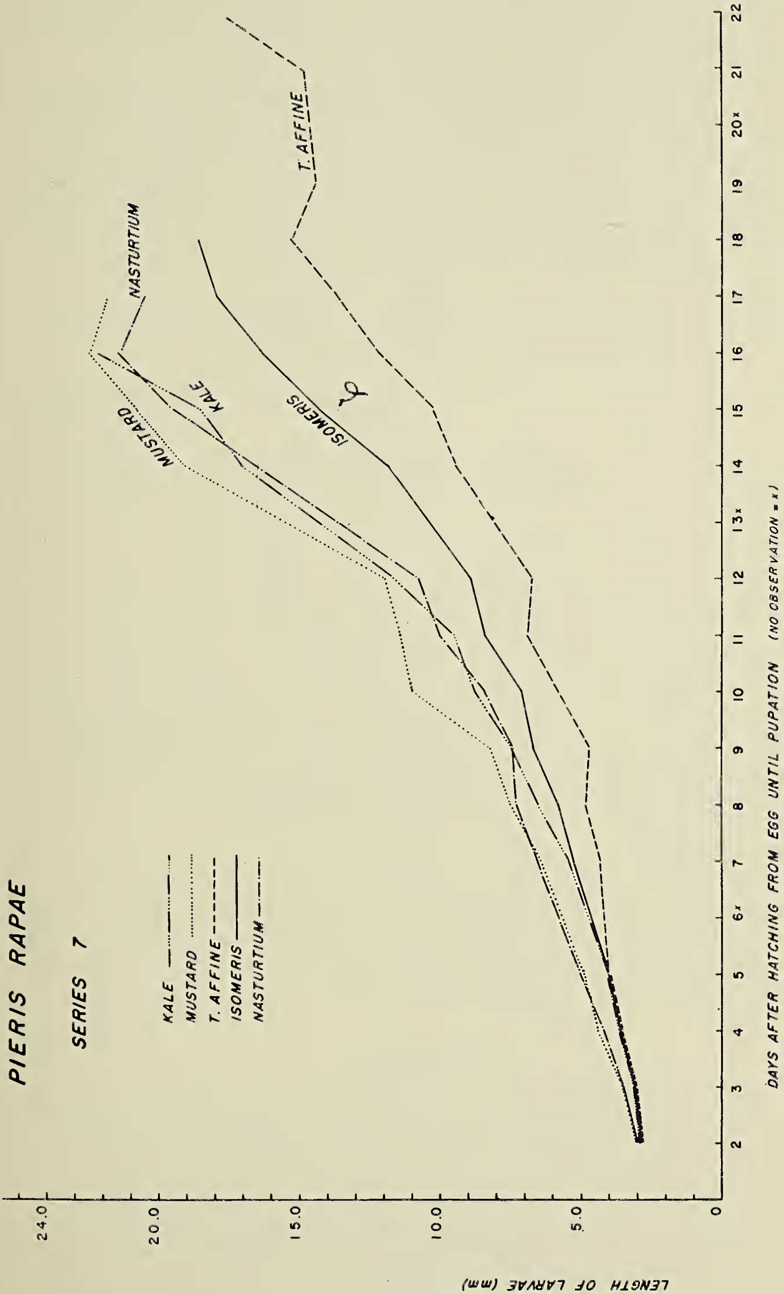
(2) Higher mortality in the tests is generally correlated with a slower development rate, a delayed time to pupation and smaller size of the larva and pupa. There are some exceptions to this rule; for example, the final size of the larva may be as great when the growth rate was slow on one plant as when it was fast on another. This has been indicated, however, only for plants of the cabbage group.

(3) Mortality rates in the various test series have been variable. These variations in mortality have been thought not only to be due to the genetic effects of inbreeding but also partly to the changed environmental conditions encountered while the tests were conducted, such as lower temperatures, etc. of the changing seasons. Lower temperatures slow the developing rate, and increase the relative humidity. Increased humidity permits the larvae to be attacked by bacterial or viral diseases to a much greater degree.

SERIES NO. 8

Tests of Series No. 8, 9 and 10 were conducted with larvae of *Pieris protodice* rather than with *Pieris rapae.*

The first series with this species (No. 8) was conducted on August 27, 1959, utilizing larvae one generation from the wild. The



7. Growth rates of larvae of *Pieris rapae* grown on various plants (Series No. 7).

females of the previous generation were obtained in a field of black mustard, not near any other source of food plant, and in which eggs and larvae were found on that plant. This is good evidence that the natural plant utilized here as larval food was mustard.

In this series, the food plants tested as larval food were mustard, kale, radish, Isomeris and nasturtium. The mortality of larvae of *Pieris protodice* on these plants increased in the order just stated, namely, 10% on mustard, 20% on kale, 55% on radish, 55% on Isomeris and 95% on nasturtium (Table 9). Deaths in the pupa stage on kale, radish and Isomeris materially increased the total mortality before adult emergence. This was not increased on mustard.

TABLE 9. Viability and growth rate of *Pieris protodice* grown on different kinds of food plants (Series 8).

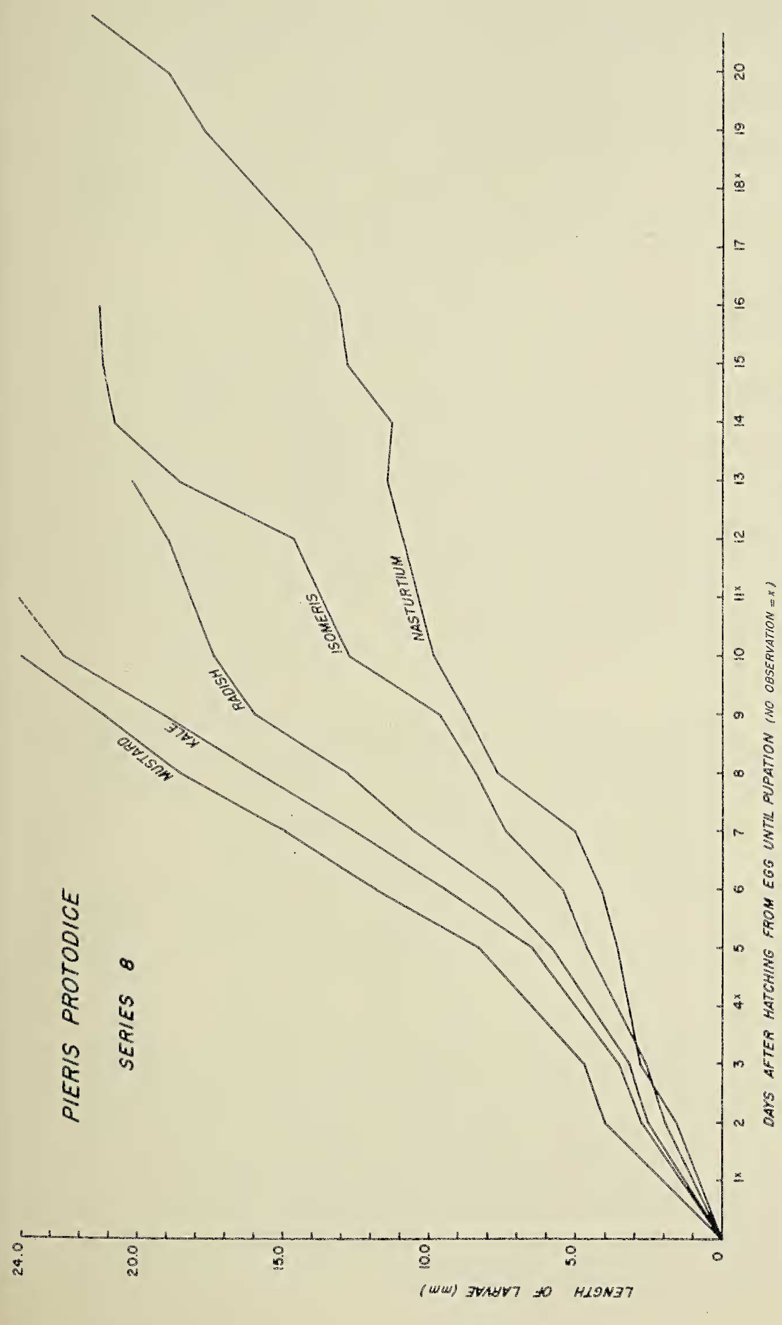
Plant	No.	No. and % of larvae died		No. and % of pupae died		Total No. and % died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	2	10%	0	0	2	10%	10	2
Kale	20	4	20%	2	10%	6	30%	11	2
Radish	20	11	55%	4	20%	15	75%	13	3
Isomeris	20	11	55%	3	15%	14	70%	16	3
Nasturtium	20	19	95%	—	—	19	95%	21	—

The length of larval life was greatly different on the various food plants, ranging from ten days on mustard, eleven days on kale, thirteen days on radish, sixteen days on Isomeris to twenty-one days on nasturtium. This wide variation in length of larval life is greatly different from anything encountered with *Pieris rapae*. It would indicate a fundamental difference in food plant adaptability between these two species, *Pieris rapae* being much more versatile in its requirements than *Pieris protodice*.

The size of the larvae at various days after hatching (Fig. 8) indicates that the mortality data are in close correlation with the size increments of the larvae with respect to food plants involved. Larvae on mustard and kale increased to 24mm in length, those on radish, Isomeris and nasturtium to 20-21mm each.

SERIES NO. 9

Discovery that *Pieris protodice* utilizes *Cleome lutea* as a natural food plant in the Owens Valley prompted a series of tests involving this plant. Both Series No. 9 and Series No. 10 were carried on for the purpose of testing *Cleome* in comparison with other plants used as standards. Series No. 9 utilized *Pieris protodice* larvae bred from adults obtained from mustard fields in the San Fernando Valley while Series No. 10 utilized *Pieris protodice* larvae obtained from *Cleome*



8. Growth rates of larvae of *Pieris protodice* grown on various plants (Series No. 8).

plants in the Owens Valley (Big Pine). There is no chance that the San Fernando population had access to *Cleome* but there is a chance that the Owens Valley population did have limited access to mustard.

TABLE 10. Viability and growth rate of *Pieris protodice* grown on different kinds of food plants (Series 9).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	6	30%	14	3
Cleome	20	7	35%	14	4
Nasturtium	20	18	90%	17	2
Isomeris	20	8	40%	17	5

The Series No. 9 larvae (Table 10) showed highest mortality on nasturtium (95%), just as in Series No. 8, with the lowest mortality on mustard (30%), next highest on *Cleome* (35%) and then Isomeris (40%). This corresponds well with comparable data in Series No. 8.

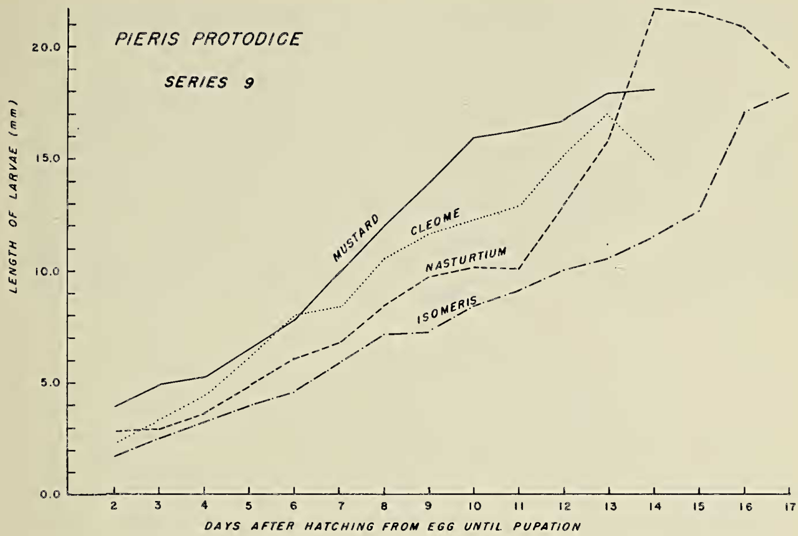
The growth increment curves for this series are somewhat comparable with the preceding series except for the one surviving larva on nasturtium which increased to a size greater than that attained by larvae on any other plant. The differences between the growth curves, however, are not as distinct and clear as in Series No. 8, perhaps because of temperature differences between the two. *Cleome* is almost as satisfactory as mustard as a food plant for these larvae. (Fig. 9).

SERIES NO. 10

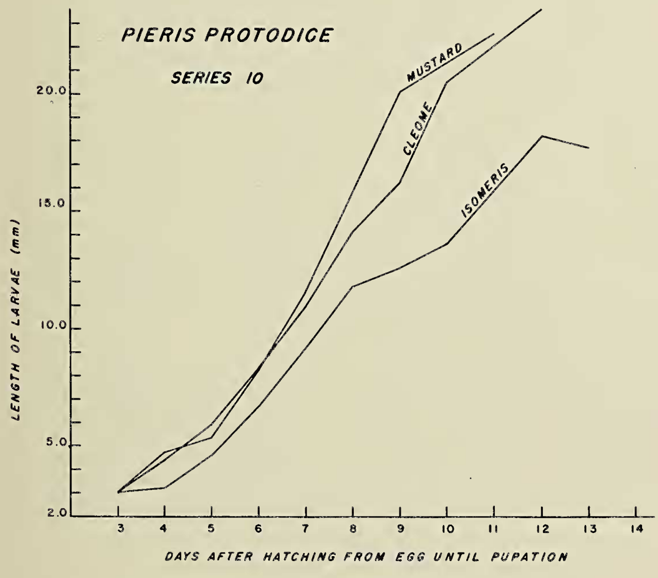
This series was run almost contemporaneously with the preceding and involved larvae from the Owens Valley strain grown on *Cleome*. The mortality (Table 11) was lowest on mustard (20%), second lowest on *Cleome* (30%) and then Isomeris (35%). There was a greater range of larval growth rates on this group of larvae on Isomeris than in any other group as well as the lowest mortality on this plant in any of the larvae tested. The growth increment curves for these larvae indicate that the larvae do not show much difference in their reaction to mustard and *Cleome* but that mustard is still slightly better, and Isomeris is always poorer. Final size of the larvae, however, was larger for the *Cleome* (23 mm) than for the mustard (22 mm) or the Isomeris (18 mm). (Fig. 10).

TABLE 11. Viability and growth rate of *Pieris protodice* grown on different kinds of food plants (Series 10).

Plant	No.	No. and % of larvae died		Days from egg to pupation	Range of variation in larval growth
Mustard	20	4	20%	11	3
Cleome	20	6	30%	12	5
Isomeris	20	7	35%	13	7



9. Growth rates of larvae of *Pieris protodice* grown on various plants (Series No. 9).



10. Growth rates of larvae of *Pieris protodice* grown on various plants (Series No. 10).

GENERAL OBSERVATIONS ON *PIERIS PROTODICE* TESTS

The three series of tests on *Pieris protodice* have indicated several significant points: (1) Larvae from strains obtained from mustard or *Cleome* populations had equally good survival value on mustard plants. The following plants gave decreasing survival value to the larvae: (Series 8) kale, radish, Isomeris and nasturtium. (Series 9) *Cleome,* nasturtium, Isomeris. (Series 10) *Cleome,* Isomeris. (2) Higher mortality in the tests is generally correlated with a slower development rate, a delayed time to pupation and smaller size of larvae and pupae.

DISCUSSION

The tests described in the preceding pages have indicated some significant information regarding the effect of various food plants on survival in two species of *Pieris.* The ability to survive on different food plants is not an all or none relationship, but rather is a relationship based upon relative ability to survive. In the most extreme case, all larvae may die rather than eat a completely unacceptable plant. On the other hand, plants may be placed in an order of desirability with regard to the ability of larvae to survive, or to grow satisfactorily, on plants which they may accept at least reluctantly.

The tests described in this report are based upon using three criteria to indicate the desirability of a plant to the larvae. The first of these is the ability to survive, or the reverse which is the mortality, expressed as a percentage of the total larvae which died during the experiment. The second criterion is the daily size increment during the life of the larva. This actually tests two factors: (1) the physiological usefulness of the food to the larvae and (2) the total amount of food eaten and uilized, which may be a direct result of the stimulatory activity of the plant toward the larvae. The third criterion is the range in variation of larval growth. The significance of this criterion is in more doubt than the other two, but the range indicated would in some degree show the genetic variability present in the larval population toward physiological adaptation to the particular plant.

The results just described show that some plants are much more suitable for larval food to certain larvae than are other plants. The reasons for this greater suitability are not made clear. In those cases where higher mortality, slower growth rate, size increments and final size are correlated, the cause of the poor growth could be lack of nutriment in the plant, or lack of larval ingestion of the plant. In other cases where larval mortality may be high, as with the broccoli, Kohlrabi and Brussels sprouts tests (Table 5) but growth rate rapid and size large (Fig. 4), there are probably two factors involved. The rapid increase in size could be due to a high attraction to a very nutritious plant, but secondary conditions surrounding the plant may be conducive to a higher mortality, namely, high water content in the plant itself, or high humidity surrounding the plant which would increase the susceptability of the larvae to virus and bacterial infections.

Toughness of leaves of a plant cannot be ruled out as a factor involved in larval speed of growth. Some leaves are too tough for the larvae to feed upon easily. Leaves of the same plant vary in this regard; succulent leaves at the shoot apex are usually much more desirable than older, mature leaves. This may be caused by toughness, or it may be caused by the greater perception of attractive substances permeating from younger leaves. At any rate, the relative uniformity of the tests in the different series is good evidence for the conclusion that this factor has not been of major significance.

The greater ability of *Pieris rapae* as compared with *Pieris protodice* to survive on a variety of common cruciferous plants is interesting in view of the fact that both succeed well on black mustard. *Pieris rapae* survives better on kale over mustard and *P. protodice* survives better on mustard over kale. However, on most other cruciferous plants tested, there was a wide disparity between their preferences. The selections made by the strains of larvae shown by these experiments complements perfectly the known differences in geographical and ecological distribution of the two species concerned, and indicates that there is little natural competition between the species for food plants. This shows also why *Pieris rapae* is always associated with European cruciferous plants, weeds or truck crops, while *Pieris protodice* is generally associated with other cruciferous plants.

Takata (1957, 1959, 1961) has published a number of papers which bear upon this problem. None of these deals precisely with the effect of various food plants on survival and growth rate of *Pieris,* but rather deals only with selection preferences by the larvae and the adult. Further considerations of the relation of this work of Takata on *Pieris rapae crucivora* to the present general program will therefore be made in a complementary paper entitled "Three Factors affecting larval choice of food plant" to be published in this journal.

A visit to our project by W. H. Dowdeswell of England during the course of these experiments was followed by a similar study of more limited extent on *Pieris napi* L. in England. Dowdeswell found that two populations of this Pierid were feeding on different cruciferous plants. By switching the food plants in laboratory experiments on testing the larvae, he found as we had, that there was a higher mortaity and decreased growth rate when the larvae were fed on plants not the normal food plant for that population (Dowdeswell and Willcox, 1961).

SUMMARY

1. Tests were made of the ability to survive of larvae of two species of Lepidoptera, *Pieris rapae* and *Pieris protodice* on various food plants.

2. Three criteria were tested: (a) mortality, (b) growth rate and size increment, (c) range in variation of larval growth.

3. Seven series of tests involving *Pieris rapae* were conducted showing the results summarized under the heading "General Observations on *Pieris rapae* Tests."

4. Three series of tests involving *Pieris protodice* were conducted showing the results summarized under the heading "General Observations on *Pieris protodice* Tests."

5. *Pieris rapae* has significantly different requirements for food plants than *Pieris protodice,* even though the tested larvae were both from mustard-bred strains.

6. The native adaptability of *Pieris rapae* to survive on various plants is better than that of *Pieris protodice.*

7. The causes of differences in survival value of the larvae on different food plants are believed to be several, but the main one is the total amount of food eaten and utilized.

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